Associated skeletal and dental remains of a fossil odontaspidid shark (Elasmobranchii: Lamniformes) from the middle eocene Lillebælt clay formation in Denmark

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A set of associated vertebrae and teeth of a fossil shark was collected from the lower Lutetian (Middle Eocene) part of the Lillebælt Clay Formation in Denmark. Its vertebral morphology indicates that the individual belongs to an odontaspidid lamniform shark. Although it is here identified as Odontaspididae indet., its tooth morphology suggests that the fossil shark possibly belongs to an undescribed taxon closely allied to *Odontaspis* or *Palaeohypotodus*. Based on comparisons with extant *Odontaspis*, the fossil individual possibly measured about 333 cm in total length. The disarticulated nature of the specimen in a low-energy deposit indicates that the shark carcass must have been lying on the sea floor for some time before its burial. The fossil individual was found along with a possible shed tooth of another indeterminate odontaspidid taxon.

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In 2007, a set of fossil shark vertebrae and teeth was collected at a Danish Middle Eocene locality on the southeast coast of Trelde Næs, north of Fredericia (GPS coordinates: N 55°36'05.2'', E 09°48'38.6''; Fig. 1). The site is situated immediately south-west of the Vesterskov Section described by Schnetler & Heilmann-Clausen (2011). The fossil assemblage was collected by three paleontology enthusiasts. Dennis Løndal Rasmussen found the first seven vertebrae and, together with Mogens Madsen, he discovered two more vertebrae in the same area two days later. One week later, he went back to the site with Søren Nielsen-Englyst to open an excavation where the rest of the vertebrae were retrieved. In addition, 20 kg of sediments were taken during the excavation and were screen-washed at the Natural History Museum of Denmark in Copenhagen by Sten Lennart Jakobsen. This yielded additional materials, including one vertebra and six tooth remains.

All the components of the fossil assemblage were found within a volume of approximately 1.5 × 1.5 m × 2 m. They are all but one tooth interpreted to come from a single individual shark because of identical morphological characteristics and preservation among the vertebrae and teeth found within the small area at a single stratigraphic horizon. The fossil assemblage is now housed in the Natural History Museum of Denmark under the catalogue number DK541 after it was declared 'Danekræ' (Christensen & Hald 1991) in 2008. Associated remains of sharks are rare in the fossil record due to the cartilaginous nature of their skeleton. The fossil assemblage that largely constitutes a single shark individual is thus significant. The aim of this paper is to describe the fossil shark and to discuss its palaeobiological significance along with another shark that co-occurred as an isolated tooth. The anatomical terminology used here largely follows Ridewood (1921) and Cappetta (1987).

Geological context

The 6 km long south-east coast of the Trelde Næs peninsula is dominated by outcrops of mainly grey-green, hemipelagic clays of the Lillebælt Clay Formation (Heilmann-Clausen *et al.* 1985). This formation spans the Lower to Middle Eocene (upper Ypresian – lower Lutetian) and its thickness at Trelde Næs is estimated to be about 70 m (Schnetler & Heilmann-Clausen 2011). The Lillebælt Clay Formation is underlain by the Ypresian Røsnæs Clay Formation and overlain by the Lutetian-Priabonian Søvind Marl Formation (Heilmann-Clausen *et al.* 1985). The Lillebælt Clay Formation holds a taxonomically diverse fauna with both epifaunal and infaunal benthos and nektonic organisms, but its shark components remain largely undescribed (Heilmann-Clausen 2012). The Lillebælt Clay Formation is composed of extremely fine-grained, smectite-rich clays informally named as 'plastic clay' and is known for forming large landslides along the coast. Its molluscan fauna indicates a water depth about 100–300 m (Schnetler & Heilmann-Clausen 2011), whereas a water depth of *c.* 500 m was assumed by Heilmann-Clausen (2012). The Lillebælt Clay Formation is subdivided into six formal beds named, in ascending order, L1 to L6 (Heilmann-Clausen *et al.* 1985). A dinoflagellate preparation (chc lab. no. 3164) was made of sideritic material associated with the fossil shark assemblage. The preparation yielded abundant, well-preserved dinoflagellate cysts. The assemblage is typical for the *Wetzeliella articulata-ovalis* Zone of Heilmann-Clausen (1988). The presence of *W. articulata* subspecies *brevicornuta* suggests that the shark-bearing horizon belongs to the lower to middle part of this zone. The zonal assignment indicates a possible provenance of the material from the upper part of Bed L4 to the lower part of Bed L6, but most likely not higher than the upper part of Bed L5. The site was visited by one of us (CHC) with Mogens Madsen in 2013. The site is located immediately south-west of a high cliff with Bed L4 referred to as the Vesterskov Section by Schnetler & Heilmann-Clausen (2011). South-west of the site occurs a high cliff with Quaternary sand and clay. Today, the layer in which the shark remains were found is covered by scree consisting of clay from Bed L5, which is seen in situ above the sliding masses. The conditions at the shark-bearing site in combination with the biostratigraphic data indicate that the shark material most likely originated from the lower Lutetian Bed L5.

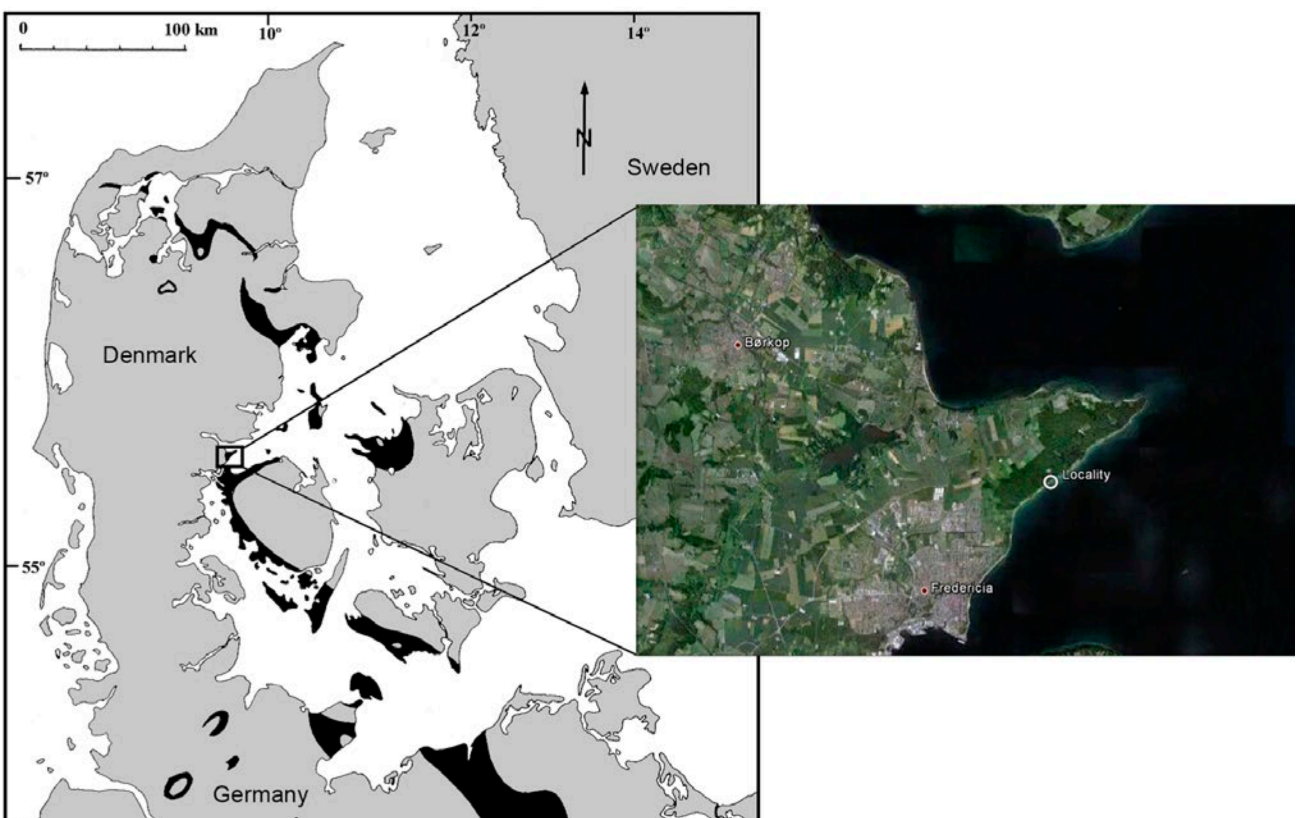

Fig. 1. Sub-Quaternary map showing, in black, the distribution of Eocene deposits in Denmark (modified from Schwarzhans 2007). The satellite image shows the excavation site at Vesterskov on Trelde Næs (modified from Google Earth (image © 2012 Aerodata International Surveys, © Google, © GeoBasis-DE/BKG, Image © 2012 GeoEye)).

Material and methods

The entire assemblage of fossil remains in DK541 comprises a total of eight teeth (five nearly complete teeth and three isolated tooth cusps) and 86 vertebrae, some of which are fragmentary (Fig. 2). Most of the vertebrae and teeth were mechanically prepared using sandblasting and scraping tools. A solution of 1 part thioglycolic acid to 19 parts water was used, as recommended by Howie (1974), to free one of the teeth (DK541d) that was embedded in a vertebra-bearing block of sideritic matrix. However, the enameloid of the tooth was severely damaged, likely due to the lack of any buffer added to the solution, and the tooth was subsequently prepared mechanically (Fig. 2B). It was therefore not attempted to free another tooth, DK541e, from its sideritic matrix (Fig. 2C).

One of the teeth in DK541, designated as DK541c, is embedded in the matrix of one of the vertebrae and exhibits only its labial side (Fig. 3). DK541c is darker in preserved colour, smaller in size, and more delicately built compared to all other teeth in DK541. Therefore, it is interpreted that DK541c does not belong to the same shark individual as represented by the rest of the specimen. For the purpose of this paper, unless otherwise explicitly indicated as DK541c, the description of DK541 and subsequent discussions specifically refer to the shark individual represented by the associated dental and skeletal remains excluding DK541c.

In order to extract additional morphological information from fragile vertebrae, computed tomography (CT) scanning was applied to eight vertebral centra using a Siemens MDCT scanner (four channels) at the Forensic Department of Rigshospitalet in Copenhagen, Denmark. The parameters for the scanning were 120 kV and 220 mA, and the algorithm Kernel 70 was used to emphasize the denser structure of the objects. The scanning was performed with a matrix of (X,Y) 0.5 mm × 0.5 mm and a reconstruction (Z) of 0.5 mm. Thus, the object is shown with isometric voxels, and proportions are kept as original. However, resolution of the scanner did not exceed 0.5 mm, and structures smaller than this size were not reconstructed. Digital cross-sections of vertebral centra were generated using

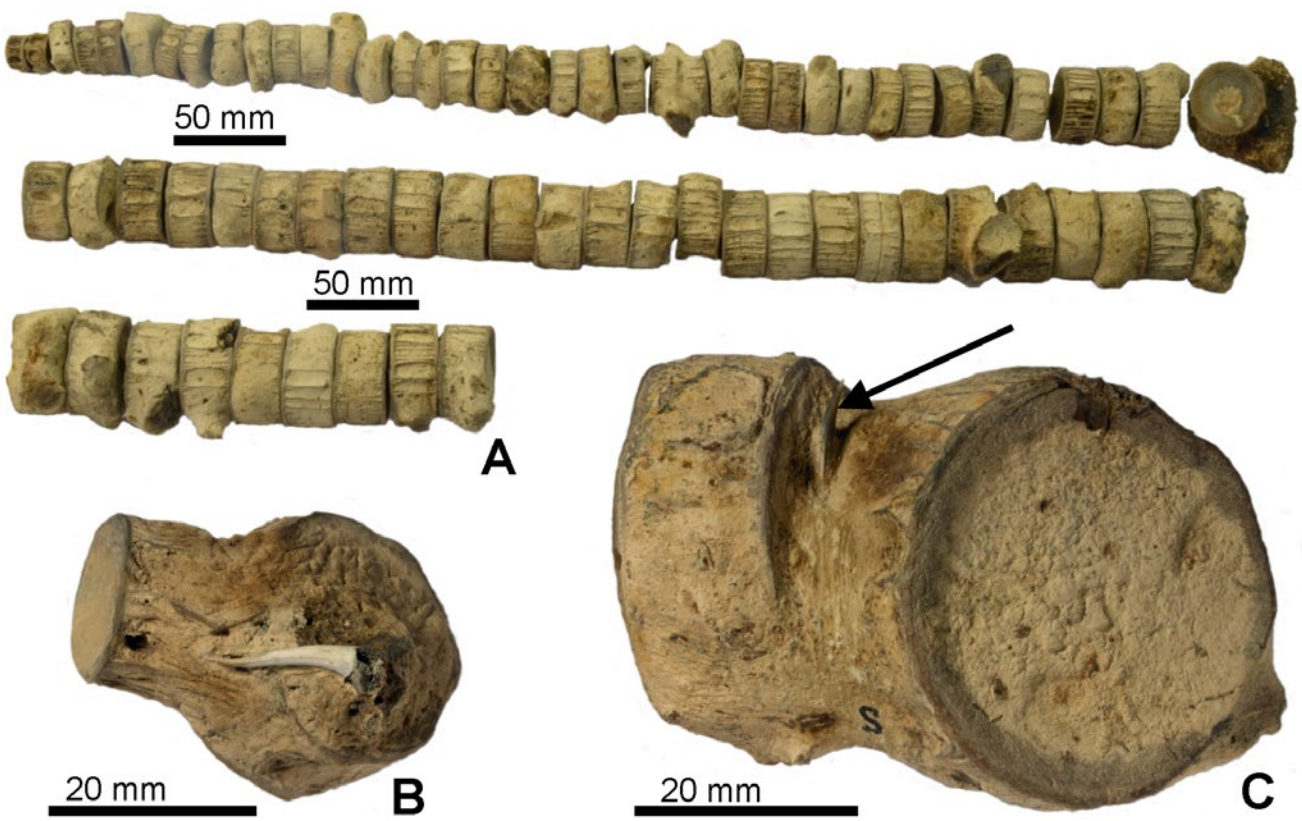

Fig. 2. Vertebral and dental remains of odontaspidid shark DK 541 from the middle Eocene Lillebælt Clay Formation of Denmark. **A**: General view of 73 vertebrae out of a total of 86. The sequence of vertebrae is artificially organized in this illustration. The rest of the vertebrae are either too fragmentary or not fully prepared (see B and C) to be included in this tentative reconstruction of the vertebral column of DK 541. **B**: Nodule DK541d containing two vertebral centra and a tooth. **C**: Nodule DK541e containing two vertebral centra and a tooth (at arrow) still embedded in the matrix between the two centra.

'AmbiVU 3D Workstation' (a free download program by AmbiVU) in which transverse sections were made through the centre of the double-cones. In addition, one of the scanned vertebrae was also cut in half in the same plane as the digital cross sections. We note that, because the teeth and the matrix have a similar density, the MDCT scanner did not allow recovery of images of the teeth still partly embedded in matrix.

Description

Vertebrae

The 86 vertebral centra are all disarticulated and are represented by various sizes (Fig. 2 and Fig. 4G–J). The largest centra measure 41 mm in lateral width, 36 mm in dorsoventral height, and 20 mm in anteroposterior thickness, whereas the smallest ones measure 18, 17, and 9 mm, respectively. The vertebrae collectively exhibit the following trend: the smaller the centrum, the more rounded it appears in anterior or posterior view. The largest ones are slightly compressed dorsoventrally, which is not the result of post-mortem compression through fossilization.

All vertebrae are amphicoelous, consisting of two evenly concave calcified cones. The rims of each centrum are relatively thick, and each concave articular face shows annuli. The two calcified cones are supported by radiating calcified lamellae that vary in number and size around the circumference of each centrum with a tendency to be arranged in pairs. In some centra, the lamellae bifurcate at their anterior and posterior extremities. On the dorsal and ventral faces, there is a pair of ovoid pits representing the basidorsal and basiventral insertion points for the neural and haemal arches, respectively. The anterior and posterior extremities of the paired pits reach to the inner surface of each vertebral cone. The dorsal pits are set closer to each other than the ventral pits.

One vertebra (DK541f) that was sectioned in a plane approximately halfway between the anterior and posterior ends reveals an asterospondylic condition (Fig. 5A). Four main uncalcified wedges are recognized, forming the basidorsal and basiventral cartilages. They radiate from the calcified primary double cone derived from the notochordal sheath. Inside the sheath, there is an uncalcified inner-zone cartilage. Between the four arch-bases, the intermedialia is invaded by calcified lamellae, which are often bifurcating towards the outside of the centrum, explaining their paired arrangement observed on the external surface. The bifurcations occur at various levels between the sheath cartilage and the external part of the centrum. This pattern is referred to as radial asterospondylic (see White 1937). All the vertebrae

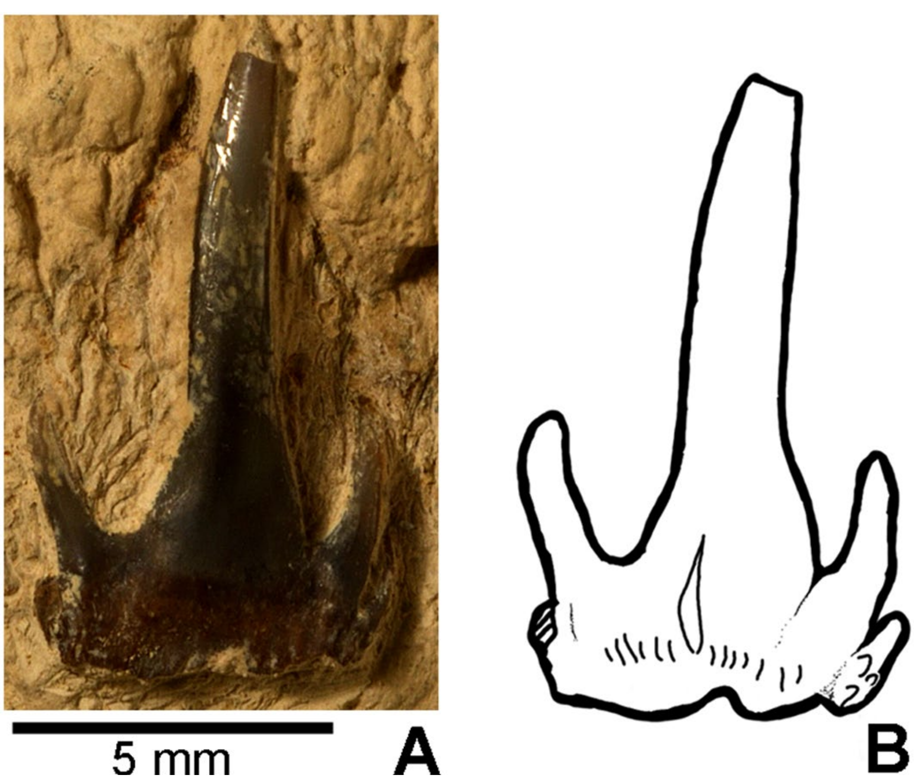

Fig. 3. Photograph (**A**) and interpretative sketch (**B**) of isolated odontaspidid tooth DK541c, labial view, that co-occurred with dental and vertebral remains of another odontaspidid individual DK541 (excluding DK541c); see Figs 2 and 4.

that were CT-scanned showed the same radial asterospondylic pattern (for rotating CT-reconstructions of DK541h, see also supplementary data files 1 and 2 on http://2dgf.dk/publikationer/bulletin/191bull61.html).

Teeth (excluding DK541c)

Each tooth, if complete, consists of a crown with a large main cusp and two pairs of lateral cusplets and a bilobed root. The crown heights of the four nearly complete teeth (DK541a,b,d,e; Fig. 4A–F) range from 10 to 24 mm, whereas the three isolated cusps have heights that range from 2.5 to 6 mm. The main cusp is tall and slender, flanked by up to two pairs of lateral cusplets. The main cusp is straight and narrow in labial view, slightly sigmoid in mesial or distal view, and slightly bulbous at its base in labial or lingual view. Both lingual and labial faces of the main cusp are convex, but the former is more convex than the latter. The mesial and distal cutting edges are sharp and reach to the crown base. The cutting edges are mostly smooth, but may bear weak serrations at the base of the main cusp. The first pair of lateral cusplets is well-developed, and they can reach up to one-third of the height of the main cusp. In contrast, the second pair is much smaller. One of the lateral cusplets in DK541a is pathologically curved lingually almost at right angle with its base (Fig. 4A–C; e.g., Becker *et al.* 2000; Balbino & Antunes 2007), and the same distinctive curvature is also seen in one of the isolated cusplets. In all teeth, the enameloid of the crown is smooth except for faint, short wrinkles or folds at the base of the labial face. At the base of the labial face of the main cusp sits a median, faint node. Each root, where preserved, shows broadly splayed lobes with narrow basal tip. The lobes are not very long and slightly curved labially. The surface texture of the root is porous except for a smooth dental band forming the tooth neck immediately below the crown on the lingual face. The lingual protuberance bears a shallow, but prominent nutritive groove with sharp edges.

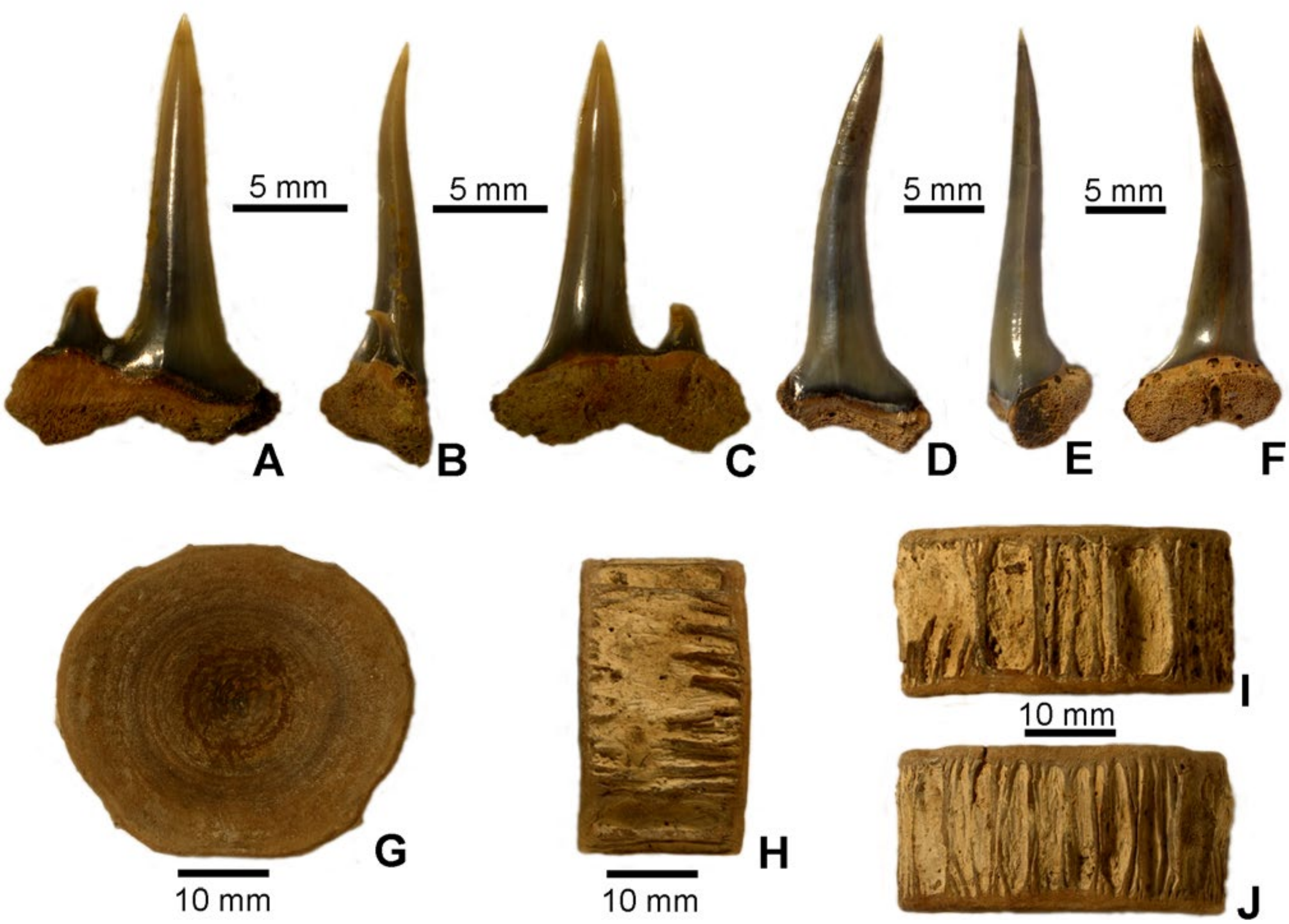

Fig. 4. Selected examples of associated dental and vertebral remains of odontaspidid shark DK541 (excluding DK541c). **A**–**C**: tooth DK541a in labial (**A**), distal (**B**), and lingual (**C**) views; **D**–**F**: tooth DK541b in labial (**D**), distal (**E**), and lingual (**F**) views; **G**–**J**: vertebral centrum DK541g in articular (**G**), lateral (**H**), dorsal (**I**), and ventral (**J**) views.

Discussion

Taxonomic remarks

All vertebrae in DK541 share the same external characteristics, and all the eight specimens that were CT-scanned show the same radial, asterospondylic structure. Asterospondylic vertebrae are restricted to the superorder Galeomorphi, and the radial asterospondylic pattern is found only in two orders, Orectolobiformes and Lamniformes (White 1937; Cappetta 1987). Orectolobiform centra depicted by Ridewood (1921) appear structurally simpler than those of Lamniformes; they have eight calcified lamellae (ten in *Stegostoma* and *Chiloscyllium*: White 1937) that are straight or branched only once or twice, and the lamellae are slightly thicker compared to those in lamniform centra. In external view, orectolobiform vertebrae show a more regular spacing of the calcified lamellae than in lamniform vertebrae (Kozuch & Fitzgerald 1989) as well as in DK541. Therefore, the vertebral morphology clearly indicates that DK541 belongs to a lamniform shark.

Based on published literature, the vertebrae of DK541 are quite similar to the vertebrae of extant *Carcharias taurus* by exhibiting a rather thick rim and ovoid ventral and dorsal pits, the extremities of which reach the rims (see Kozuch & Fitzgerald 1989; Purdy *et al.* 2001). However, we note that the centra of DK541 (Fig. 4G–J) also closely resemble those of extant *Odontaspis ferox* (Fig. 5C–F) not only externally, but also internally (Fig. 5A–B). Centra of other extant lamniform sharks, such as *Isurus*, possess very thin rims, and those of *Carcharodon* possess shorter ventral and dorsal pits, the extremities of which do not reach the rims (Kozuch& Fitzgerald 1989). This latter character seems, however, quite variable as the extremities of the dorsal and ventral pits do reach the rims in the vertebrae of *Carcharodon hubbelli* from the Pliocene of Peru (Ehret *et al.* 2009, 2012). The vertebrae of *Otodus obliquus* from the Eocene London Clay figured by Casier (1966) are twice the size of DK541, and the extremities of the dorsal and ventral pits do not reach the rims. It should also be noted that the vertebrae of DK541 do not belong to any of the Cretaceous lamniforms with known vertebral morphologies, such as Cretoxyrhinidae and Cardabiodontidae, because these taxa have more numerous lamellae in the lateral intermedialia, and the entire centra are anteroposteriorly compressed (e.g., Siverson 1999; Blanco-Piñón *et al.* 2005; Shimada *et al.* 2006).

DK541 is also interpreted to be a lamniform shark on the basis of its teeth with well-developed root lobes, tall slender main cusp, and sharp lateral cusplets.

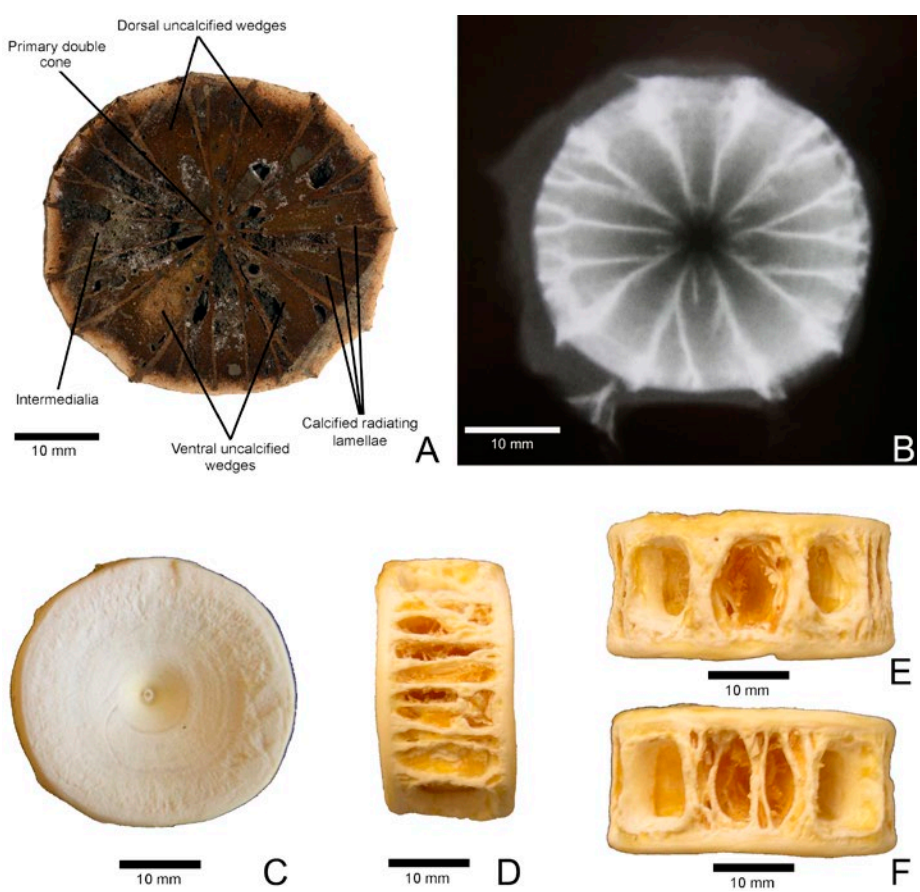

Fig. 5. **A**: Sectioned fossil vertebral centrum DK541f. **B-F**: internal and external morphology of the sixth vertebra removed from 297-cm-total length extant *Odontaspis ferox* (BPBM 9335); **B**: x-ray image; **C**: articular view; **D**: lateral view; **E**: dorsal view; **F**: ventral view.

The root lobes are well separated and the lingual protuberance bears a distinct nutritive groove. Such characteristics can be found in the teeth of the family Mitsukurinidae and Odontaspididae *sensu lato* (i.e., a paraphyletic assemblage including Odontaspididae and Carchariidae: Heinicke *et al*. 2009; Vélez-Zuazo & Agnarsson 2011). However, teeth of mitsukurinids tend to exhibit a more prominent lingual ornamentation and more reduced lateral cusplets than those of odontaspidids and DK541 (see Cappetta 2012). When compared to other Eocene odontaspidids, the teeth of DK541 can be distinguished easily from those of *Araloselachus, Borealotodus, Carcharias, Glueckmanotodus, Hypotodus, Jaekelotodus, Mennerotodus, Sylvestrilamia*, and *Turania,* in which the teeth do not possess lateral cusplets as tall as in DK541 (see Cappetta 2012). Well-developed lateral cusplets occur in *Brachycarcharias, Odontaspis, Orpodon*, and *Palaeohypotodus* (Cappetta 2012). Teeth of *Brachycarcharias*, however, possess a broader main cusp and cusplets than those of DK541, and the lingual face of their main cusp is ornamented (Cappetta & Nolf 2005). Teeth of *Orpodon* are much smaller (<12 mm in height) and possess broader lateral cusplets than those of DK541 (see Cappetta & Nolf 2005; Cappetta 2012).

DK541a and DK541b (Fig. 4A–F) possess cutting edges that reach the base of the main cusp that is quite compressed labiolingually, characteristics not consistent with *Odontaspis winkleri* and the genus *Odontaspis* in general (see Cappetta & Nolf 2005; Mannering & Hiller 2008; Cappetta 2012). The weak serrations at the base of their cutting edges are more reminiscent to those observed in *Palaeohypotodus* (Cappetta 2012), but this genus is unknown after the Ypresian (Ward & Wiest 1990; Cvancara & Hoganson 1993). Another odontaspidid species, *O. speyeri*, possesses vertical folds and tubercles at the labial crown base in juvenile specimens, possibly indicating its close phylogenetic affinity to *Paleohypotodus* (Siverson 1995). Teeth of *O. speyeri,* however, have relatively short lateral cusplets and less slender crowns compared to the teeth of DK541 (see Arambourg & Signeux 1952). Moreover, *O. speyeri* has only been found in early Paleocene deposits, whereas DK541 comes from the lower Lutetian (Arambourg & Signeux 1952).

In summary, although the resemblance between *Carcharias* vertebrae and the vertebrae of DK541 does exist, vertebrae of DK541 are also morphologically quite similar to those of *Odontaspis ferox*. The tooth morphology seen in DK541 suggests that the shark individual belongs to an odontaspidid close to *Odontaspis* or *Palaeohypotodus*. Because the tooth morphology observed in DK541 is quite unique, it may belong to an undescribed odontaspidid species. However, the tooth set in the specimen is small, making it difficult to adequately decipher the total morphological range of teeth. Therefore, we here conservatively identify DK541 as Odontaspididae indet. that was closely allied to *Odontaspis* or *Palaeohypotodus*.

Body size estimation

The biology of the fossil shark individual (DK541) is difficult to infer especially because of its tenuous taxonomic identity and incompleteness. However, we here estimate the total length (TL) of the fossil shark in life based on two extant odontaspidid (*Odontaspis ferox*) specimens, BPBM 9334 and 9335, housed in Bernice P. Bishop Museum, Honolulu, Hawaii, USA. BPBM 9335 preserves only the head region from a 297-cm-TL individual (sex unknown) in which its sixth vertebra has a diameter of 30 mm. On the other hand, BPBM 9334 is a complete 190-cm-TL female, and its skeleton imaged through computed tomography (CT) reveals that the thirty-third vertebra has the largest centrum and is 1.22 times larger than its sixth vertebra. Thus, the unpreserved thirty-third vertebra in BPBM 9335 likely had a diameter of 36.6 mm (note: exact vertebral measurements in BPBM 9334 cannot be taken from CT images and thus both specimens are needed for our calculation). The largest vertebra in DK 541 has a diameter of 41 mm, which is 1.12 times larger than the inferred diameter of the largest vertebra in BPBM 9335. If the preserved fossil vertebra is assumed to be the largest vertebra in the fossil individual, and if the body form as well as the relationship between the body form and vertebral properties in the fossil shark are assumed to have been the same as in the extant shark, the fossil individual possibly measured 333 cm TL.

The tallest tooth in BPBM 9335 is the second lower anterior tooth (sensu Shimada 2005), and its vertical crown height (CH) is 26 mm. The tallest preserved tooth in the fossil specimen is DK541b, which measures 24 mm CH. Its rather erect crown suggests that it likely represents one of the anterior teeth, but it was likely not the tallest anterior tooth in the dentition because of its sinuous crown. Its CH of 24 mm means that the tooth is 92% of the tallest tooth in BPBM 9335, and this percentage would yield an estimated TL of 274 cm for the fossil shark. This estimated TL is shorter than the TL estimated from the largest vertebra (see above), but this can be explained by the fact that DK541b may not have represented the largest tooth in the fossil individual. Therefore, whereas the tooth-based TL estimation would at least suggest that the fossil shark individual was no smaller than 274 cm TL, we consider the vertebra-based estimation (i.e., *c*. 333 cm TL) to be closer to the actual length of the fossil shark in this particular instance.

Taphonomic remarks

The shark individual represented by associated teeth and vertebrae (DK 541) was found with a tooth (DK541c; Fig. 3) presumably from another shark individual (see above). It is an incomplete tooth preserving only the crown with a main cusp and three cusplets in labial view. The tip of the main cusp is missing but the tooth has an estimated total apicobasal crown height of 10.5 mm with the following characteristics: cutting edges restricted to the narrow uppermost part of the main cusp that widens rapidly mesiodistally towards its base; labial surface flat; one medial pair of high, narrow, and diverging lateral cusplets flanking the main cusp, with height one-third of that of the main cusp and tips bent slightly towards the main cusp; a second (distal) pair of lateral cusplets (one side is missing) similar in shape to the medial pair but with height half of that of the medial pair. Well-developed ridges ornament the base of the labial face under the two mesial cusplets present and form minute tubercles, some of which are arranged on top of one another (the presence of this feature is uncertain on the distal side due to poor preservation). The crown surface is smooth except for a median, faint node at the base of the labial face of the main cusp. The well-developed labial ornamentation at the base of the crown in DK541c is similar to that in *Palaeohypotodus rutoti* (Leriche 1902; Gurr 1962; Cappetta 2012), but the narrow aspect of the main cusp and cusplets is found only in juvenile specimen of this species (Leriche 1951). Furthermore, the stratigraphic range of the genus does not extend over the Ypresian. We therefore leave this tooth in open nomenclature as a second Odontaspididae indet. To note, the estimated crown height of 10.5 mm is only about 40% of the crown height of the tallest tooth in BPBM 9445, giving an estimated TL of 120 cm; this is a distinct minimum value because the tooth likely did not represent the tallest tooth in the dentition.

The occurrence of a tooth from another shark individual with DK541 is taphonomically intriguing. The rock in which the fossil assemblage occurred is composed of fine-grained clays (see above), indicating deposition in a low-energy environment. Because the components of DK541 were all disarticulated and scattered across the sediment, it suggests that the shark carcass must have been lying on the sea floor for some time (e.g., see Schäfer 1972). Because DK541c is represented by a single tooth with no apparent association with other odontaspidid elements found together, it likely represents a shed tooth. The association of DK541c with the skeletal remain of DK541 may be coincidental, but it could be a result of feeding. However, extant odontaspidid sharks do not typically scavenge large animal carcasses (e.g., Compagno 2001) and DK541c seems too delicate to effectively tear off pieces of flesh of a large shark such as DK541. Therefore, if DK541c indeed represents a shed tooth, it could possibly be from feeding on smaller animals that were feeding on the shark carcass.

Conclusion

DK541 from the lower Lutetian part of the Lillebælt Clay Formation in Denmark is determined to be an odontaspidid lamniform shark based on vertebral and dental characteristics. Its tooth morphology suggests that the shark may belong to an undescribed odontaspidid taxon closely allied to *Odontaspis* or *Palaeohypotodus*, but we here conservatively refer to it as Odontaspididae indet. The fossil shark individual was likely no smaller than 274 cm total length based on the largest preserved tooth compared to teeth in extant *Odontaspis ferox*. However, comparison of vertebral sizes between the largest preserved vertebrae in DK541 and that in extant *O. ferox* suggests that the fossil individual possibly measured as much as 333 cm total length. The disarticulated nature of the skeletal and dental components of DK541 in a low-energy deposit suggests that the shark carcass must have stayed on the ocean floor for some time. The fossil individual represented by DK541 was found with a possible shed tooth of another odontaspidid (DK541c) that was likely a smaller individual than DK541.

Acknowledgments

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